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Monophyly and phylogenetic position of the Diplura (Hexapoda)

M. Koch

Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany

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Summary. The structure of the head and mouthparts of the so-called Entognatha were compared. Two different types of entognathy, presumably of independent origin, were differentiated. One form is characteristic of the Ellipura (= Collembola + Protura) while the second is found in the Diplura. The entognathous condition in campodeids and japygids shows remarkable similarities in detail, e.g. in the form of the head skeleton and the fusion of the first maxillae with the hypopharynx. Hence, the Diplura are presumed to form a monophyletic group. The reduction of the gonopods and the formation of a genital papilla, as well as the fusion of the abdominal segments X and XI, are regarded as further possible autapomorphic characters of the Diplura. The traditional "Entognatha" are considered, however, to be a paraphyletic assemblage. The Ellipura form the sister taxon of all other insects; the Diplura constitute the adelphotaxon to the Ectognatha.

Key words: Diplura, phylogeny, Ellipura, entognathy

Introduction

The Diplura have been united, traditionally, with the Ellipura (= Collembola + Protura) to form the so-called Entognatha. Entognathy has been supposed to be a synapomorphic character of these groups and was considered to have arisen only once within the primarily wingless insects. Accordingly, the "Entognatha" are believed to form the sister group to all other insects. These represent a monophyletic unit, the Ectognatha (with Archaeognatha and Dicondylia [= Zygentoma + Pterygota]). However, the monophyly of the "Entognatha" has recently been questioned (e.g. Kukalová-Peck 1987; Stys et al. 1993). The crucial question concerns the monophyly and phylogenetic position of the Diplura. Here, evidence is presented that the previous "Entognatha" form a paraphyletic assemblage. The Diplura are maintained as a presumably monophyletic unit and are regarded as the adelphotaxon of the Ectognatha.

Entognathy within the "Entognatha"

Studies on functional morphology of the head and mouthparts have demonstrated (pers. observ.) that two different types of entognathy, presumably of independent origin, can be differentiated within the "Entognatha".

The entognathous condition of the **Ellipura** is characterized by: **(i)** labium (= fused maxillae II) differentiated only antero-ventrally on the head capsule; **(ii)** formation of a median groove (*linea ventralis*) on the ventral side of the head capsule; **(iii)** mandibles and first maxillae hidden in separated paired gnathal pouches; **(iv)** mandibles with basic condylus and ligament connecting the base of the mandibles with the lateral wall of the head capsule (plesiomorphic (!) state retained).

In contrast, entognathy in the **Diplura** differs as follows: **(i)** labium extends caudad to the foramen magnum; **(ii)** an additional sclerite (*admentum*) is differentiated latero-ventrally on each side of the head capsule; **(iii)** base of mandibles and first maxillae in a single paired mandibulo-maxillary gnathal pouch; **(iv)** basic condylus of the mandibles and mandibular ligament reduced; **(v)** first maxillae and superlinguae connected and partly fused.

Further, details of the endoskeleton are remarkably similar in campodeids and japygids (no "anterior tentorial apodeme"; superlingual-sclerites fused with fulturae).

Conclusions

Ectognathy is generally accepted to be the plesiomorphic state. The head and mouthparts (a) of the Ellipura, and (b) of the Diplura show different combinations of plesiomorphic and apomorphic characters. Both types of entognathy are so different that one alternative cannot be regarded as the more primitive basis for the evolution of the other. Hence, the hypothesis of an anagenetic development of entognathy in a sequence Japygina, Campodeina, Ellipura (Stys & Bilinski 1990) is rejected. Entognathy as such cannot be considered any longer to be a synapomorphy of Ellipura and Diplura, as the two different arrangements cannot be traced back to a common ground pattern. Reconstructing a common ancestor of this kind would lead to a non-functional concept. Instead, the available arguments support the view that entognathy, in primarily wingless insects, had arisen independently at least twice: in the stem lineage of the Ellipura, and in the stem lineage of the Diplura. Highly specialized and almost identical entognathous conditions exist in campodeids and japygids. This justifies the view that the Diplura really form a monophyletic unit, but the "Projapygoidea" will need further examination.

Phylogenetic interrelationships

Monophyly of the Diplura

Arguments for the maintenance of the Diplura are as follows:

(i) *Special type of entognathy* [Fig. 1: *19*]. – As described above, the cephalon of campodeids and japygids is characterized by impressive similarities. This entognathic condition can hardly be regarded as having arisen convergently.

(ii) *Genital papilla* [Fig. 1: *20*]. – In both sexes, a retractile genital papilla is differentiated between abdominal segments XIII and IX; it bears the unpaired gonopore. The legs on these segments (gonopods) are reduced (no styli/coxal vesicles); vestigial genital appendages are known only in male japygids (Pagés 1989). In contrast to this, gonopods exist in the Protura (*squama genitalis*; François & Dallai 1989), as well as in the Archaeognatha and Zygentoma (composed of coxopodites + styli + gonapophyses; Bitsch 1974).

(iii) *Only 10 abdominal segments visible* [Fig. 1: *21*]. – Differentiation of 11 abdominal segments (+ Telson) is postulated for the ground pattern of the Hexapoda (Hennig 1969). This condition is retained in the Protura as well as in the Archaeognatha and Zygentoma. However, in the Diplura, only 10 abdominal segments are visible. Posteriorly, the 10th urite is followed by the cerci [= legs of the XIth (!) abdominal segment; they articulate in the Diplura with the sternum and tergum of the 10th urite] and the so-called anal valves. The whereabouts of abdominal segment XI and of the telson are not yet definitively clear. In any case, the special way in which the abdomen is differentiated (with only 10 segments visible) is regarded as an autapomorphic feature.

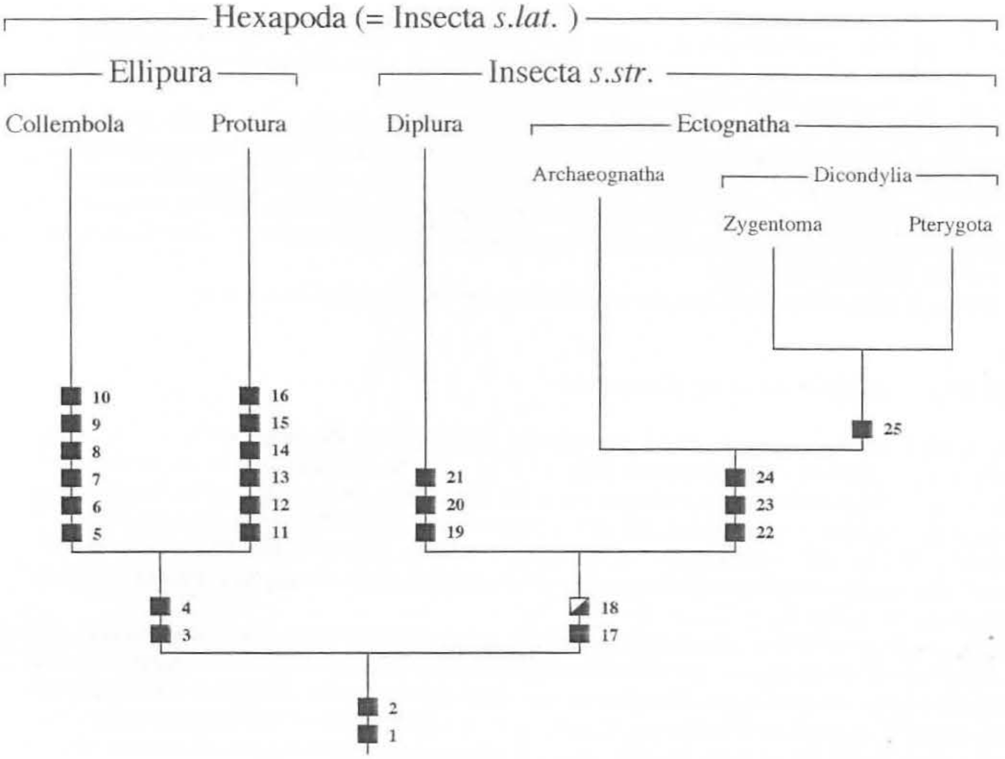

Fig. 1. Phylogenetic relationships of higher subtaxa of the "Apterygota": argumentation scheme. – *Closed boxes* indicate apomorphies; *numbers* refer to characters listed below (see *list of characters*). List of characters: **(1)** Thorax comprising 3 thoracomeres bearing 3 pairs of locomotory limbs. **(2)** 11 abdominal metameres. **(3)** Linea ventralis. **(4)** Special type of entognathy [different from (19)]. **(5)** Neotenic: only 6 abdominal segments. **(6)** Specialized abdominal appendages: ventral tube, retinaculum, furca. **(7)** Compound eyes primarily reduced to 8 single, isolated ommatidia. **(8)** Antennae primarily composed of 4 antennomeres; no antennal vessels. **(9)** Tibiotarsus. **(10)** Central nervous system condensed: all abdominal ganglia incorporated into the metathoracic ganglion. **(11)** Loss of antennae. **(12)** Prothoracic legs transformed into functional "antennae"; coincidently (i) head capsule shifted backwards onto the prothoracic segment, (ii) subpharyngeal ganglia complex fused with prothoracic ganglion. **(13)** Compound eyes completly reduced. **(14)** Fulcro-tentorium. **(15)** *Squama genitalis* hidden in genital chamber which opens between abdominal segment XI and telson. **(16)** Paired abdominal defense glands with covered openings at the hind border of the VIIIth tergite. **(17)** Epimorphic development. **(18)** Loss of temporal organ. **(19)** Special type of entognathy [different from (4)]. **(20)** Genital papilla with unpaired gonopore between abdominal segments XIII and IX (gonopods reduced). **(21)** Only 10 abdominal segments visible. **(22)** Antennae composed of 3 antennomeres, the distal one annulated. **(23)** Ovipositor formed by gonapophyses on abdominal segments VIII and IX. **(24)** Annulated "terminal filament" developed from dorsum XI. **(25)** Dicondyly of the mandibles.

Rejection of the Entognatha/Ectognatha concept

As stated above, the character "entognathy" as such does not justify a taxon called "Entognatha" (with Ellipura and Diplura). The same is true with regard to the following characters; they have been believed to support the assumed monophyly of the "Entognatha" (Hennig 1969):

(i) *Reduction of compound eyes.* – Reduction or transformation of the compound eyes represents a widly spread phenomenon within the Tracheata. In general, it correlates with cryptozooic life habits. This may also have happened several times independently within the "Entognatha". Accordingly, low value is attributed to this character.

(ii) *Reduction of Malpighian tubules.* – The homology of the Malpighian tubules in tracheates has not yet been established. It is possible that these structures originated more than once. Within the "Entognatha", Malpighian tubules in protures and campodeids are represented by short papillae. They are totally lacking in collembolans and japygids. So far, it is not possible to decide whether the Malpighian papillae in proturans and campodeids are vestiges, oriments or even of independent origin.

There is no convincing argument for maintaining the "Entognatha" as a taxon.

Diplura as adelphotaxon of the Ectognatha

One sound argument favours the view that the Diplura form the sister group of the Ectognatha, i.e. epimorphic development [Fig. 1: *17*]. – In the Diplura as well as in the Ectognatha, *all* abdominal segments are present at the first instar. In contrast to this, the development in the Protura is anamorphic: the abdomen is supplemented by additional segments after hatching. Within the "Myriapoda", epimorphosis is only known in the Epimorpha (Chilopoda). Hence, anamorphosis represents the plesiomorphic state; among hexapods it was only retained in the Ellipura. → but not in Collembola

Another feature which is regarded as a potential autapomorphic character of the Insecta *s.str.* (= Diplura + Ectognatha) is the loss of temporal organs [Fig. 1: *18*]. – Structurally similar sensory organs in the temporal region of the head are known in all higher subtaxa of the "Myriapoda" (organs of Tömösváry, Pseudoculi) as well as in the Collembola (postantennal organ) and also in the Protura (Pseudoculus). In all instances, these organs are connected with the protocerebrum (Altner & Thies 1976). Organs of this type are generally lacking in the Diplura and in the Ectognatha. This may be regarded as a synapomorphic feature of these groups, but the homology of the temporal organs should be expressively confirmed.

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